A Double Spore Wall in Macroglossum

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Since the original description of *Macroglossum alidae* by Copeland (1909a, p. 343; 1909b, p. 9), little has been learned about this strange and primitive member of the Marattiales. Campbell (1911, 1914a, 1914b) has dealt with the anatomical aspects of the gametophytes and sporophytes but, surprisingly, he gives no description of the spores. In Erdtman (1957, p. 79), the proximal and distal faces of *M. alidae* are illustrated both in surface view and in optical section; the spore is globose but distally flattened, with an irregular and sparsely tuberculate exine. Kremp & Kawasaki (1972, p. 4) described the spores from seven specimens as rounded-triangular (32.4 × 28.7 μm), trilete, and scabrate.

The observation of spores of *M. alidae (Molesworth-Allen 3197,* US) under the SEM shows a regularly and densely tuberculate-subbacillate perispore *(Fig. 1),* the shape and dimensions of which are in agreement with the foregoing authors. An unusual case of double-walled spores is shown in *Fig. 2,* a preparation from the same specimen. In it, the outer exine layer is cracked to reveal a smaller but morphologically perfect spore inside, one per "parent spore." This phenomenon is hitherto unreported in the fern literature but may not be rare, for we have observed a "parent spore" of *Botrychium* sp. containing four "daughter spores," and it is quite possible that such "angiospores" occur in other pteridophytes.

The biosystematic implications of angiospore production are, as yet, unknown. Research is needed to elucidate various questions that come to mind, including: (a) What, if any, percentage of angiospores is viable? (b) What is their genotype and resulting phenotype? (c) What is the ploidy level of angiospores in relation to "parent spores"? (d) Do angiospores represent a reduction mechanism for polyploidal pteridophytes? (e) Within a sporangium, what percentage of "parent spores" contain angiospores? (f) What effect would this ratio have on the population structures of the resulting gametophytic and sporophytic generations? (g) Does the smaller size the angiospores have any effect on the range and pattern of their dispersibility? (h) Is angiospory a primitive trait only to be found in eusporangiate pteridophytes?

Spore size and shape, of themselves, are not indicative of viability. Recent literature abounds with examples of the germination of supposedly non-viable abortive spores in hybrids and of larger than normal diplospores formed through ameiotic apogamy. At present, questions (b) and (d) are unanswerable due to the lack of appropriate materials. The fact that the cytology of *Macroglossum* has never been investigated prevents speculation on whether angiospores represent any change in ploidy level, be it reduction or augmentation. The Marattiales have high chromosome numbers as do the Ophioglossales, the only other instance in which we have as yet observed angiospory. Until a large enough quantity of both "parent spores" and angiospores are cultured, questions (e) and (f) also remain unanswerable.

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The Marattiales show a high degree of endemism; *Macroglossum,* for instance, is confined to Borneo. It is logical to assume that smaller spores, such as angiospores, might be more easily dispersed. On the other hand, smaller spores could be short-lived, reducing their dispersibility and enhancing endemism. The genus *Botrychium* is cosmopolitan, but throughout its range its species show complex patterns of geographically separated cytological races. This genetic variation may be partly responsible for the taxonomic chaos within the genus. It may be that angiospory is related to these races.

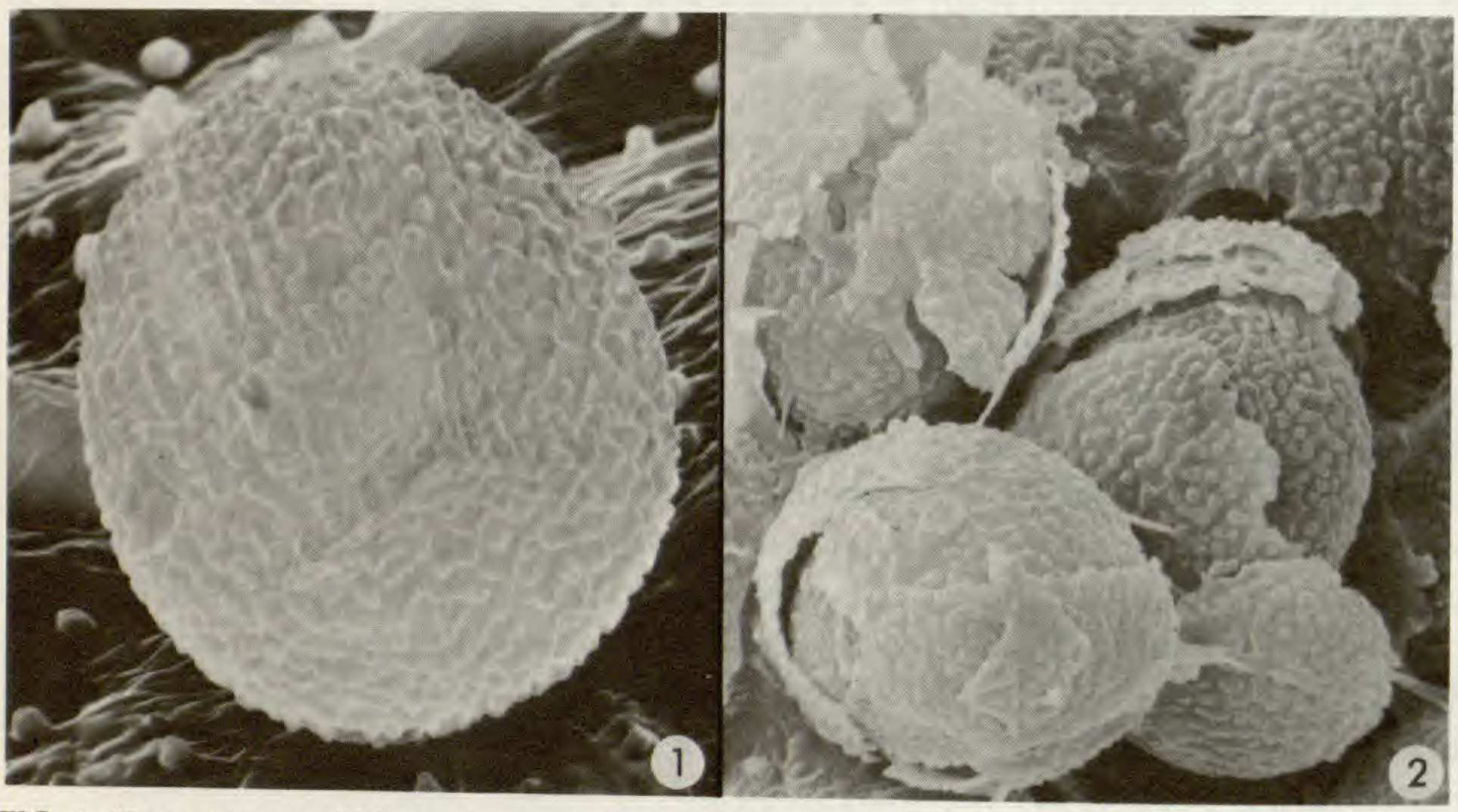

FIG. 1. Normal spore of *Macroglossum alidae,* × 3075. FIG. 2. Double-walled spore of *M. alidae,* × 1535.

The fact that angiospores have so far been observed only in the Marattiales and Ophioglossales might have one of three explanations: chance observation due to the much higher number of spores per sporangium; angiospores have been overlooked in the more advanced leptosporangiate pteridophytes; or within the pteridophytes, angiospory is a trait exclusive to the eusporangiate members.

The phenomenon of angiospory may well represent a new sub-pattern in the life cycle of pteridophytes.

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